A HISTOLOGICAL STUDY OF SYNDISYRINX FRANCISCANUS, GEN. ET SP. NOV., AN ENDOPARASITIC RHABDOCOEL OF THE SEA URCHIN, STRONGYLOCENTROTUS FRANCISCANUS [1]

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Introduction

Up to the present time eight genera of worms endoparasitic in echinoderms and sipunculids have been described that belong to the rhabdocoel family Umagillidae Wahl, 1910b. Schneider described the first species, *Anoplodium parasita*, in 1858. Since then six questionable and three valid species of this genus have been reported from widely separated localities as parasites of holothurians. Their distribution extends from the Mediterranean, Ionian, and North Seas to Japan and the Philippines (Bock, 1926). *Syndesmis echinorum* Francois, 1886, the only species of the genus, is found in echinoids. It has been collected in the Mediterranean (Russo, 1895), Norway (Westblad, 1926), and the English Channel (Braun, 1889). Three species of the genus *Collastoma* are found in sipunculids at Roscoff (Dörler, 1900), the Gulf of Kola (Beklemischev, 1916), and the Bay of Naples (Wahl, 1910a). The genus *Desmote* is represented by one species, *D. vorax*, discovered in a crinoid collected in the Gulf of Kola (Beklemischev, 1916). A single species parasitic in holothurians has been described in each of four genera, i.e., a Japanese form, *Xenometra arbora* Ozaki, 1932, and three reported from the coast of Norway, *Wahlia macrostylifera* Westblad, 1930, *Anoplodiera voluta* Westblad, 1930, and type genus *Umagilla forskalensis* Wahl, 1909.

The only reference to a member of the Umagillidae from the Western Hemisphere was made by Powers in 1936. He reported the presence of a Syndesmis-like worm in the coelomic cavity of the echinoid, *Centrechinus antillarum*, at Tortugas. A complete description was not given; however, as compared with *Syndesmis*, noticeable differences were observed in details of the copulatory apparatus and the arrangement of the shell glands. While the endoparasitic rhabdocoel of *Strongylocentrotus franciscanus*, the large common sea urchin of the California coast, is well known to some investigators who have worked at Pacific Grove, a description of this worm has not been recorded in the literature prior to the present account.

[1] This work was done at the Wilson Zoological Laboratory of the University of North Carolina in partial fulfillment of the requirements for the degree of Master of Arts. The author is indebted to Professor D. P. Costello for suggesting the problem, for the slide preparations upon which this study was essentially based, and for the invaluable suggestions and criticisms rendered during the preparation of this paper. The author wishes to acknowledge his appreciation to Dr. L. H. Hyman for many valuable recommendations and for permission to introduce her revised and hitherto unpublished terminology relating to this group. To Miss Catherine Henley the author expresses his gratitude for the translation of a number of the references cited herein.

[2] Now in the School of Biological Sciences of Stanford University.

Systematic position[3]
Order Rhabdocoela
Suborder Lecithophora
Section Dalyellioida
Family Umagillidae Wahl, 1910
Subfamily Umagillinae Wahl, 1910
Genus Syndisyrinx, gen. nov.
Genotype Syndisyrinx franciscanus, sp. nov.

Holotype. A whole mount in the United States National Museum, Washington D. C.

Repositories of type material. In each of the following repositories a whole mount, a transversely sectioned, and a sagittally sectioned preparation selected from the type material have been deposited: U. S. National Museum, Washington, D. C.; American Museum of Natural History, New York City; British Museum, London; California Academy of Science, San Francisco; Wilson Zoological Laboratory of the University of North Carolina; and Museum of Natural History, Stanford University. Additional preserved material may be obtained from the author or from any of these institutions.

Type locality. Mussel Point, Monterey Peninsula, California, Lat. 36°, 37′, 20″ N., Long. 121°, 54′, 15″ W.

Collectors. D. P. Costello, 1937 and H. E. Lehman, 1945.

Distinguishing characteristics. Umagillinae with a single intestine, paired and branched ovaries, cuticular penis, and a bursa seminalis connected by cuticular ducts to the seminal receptacle and bursal canal.

Materials and Methods

Fifty-four rhabdocoel parasites were obtained from two specimens of the sea urchin *Strongylocentrotus franciscanus* (A. Agassiz) by Dr. D. P. Costello in August 1937 at Pacific Grove, California. These specimens were fixed in Heath's, Boveri's, Lillie's and Worcester's solutions. Five of the individuals were sectioned serially at 10 μ and stained with Heidenhain's iron hematoxylin and orange G. One of these preparations was exceptionally fine and the majority of the accompanying figures were made from it. Unfortunately this preparation, which the author intended to designate as the holotype, was lost when a microscope was stolen. This material, including the slide preparations, was turned over to me by Dr. Costello. The morphological study was based on this material.

In the summer of 1945 during June, July, and August, the author collected several hundred additional specimens from the same locality. Over sixty urchins were examined and all were found to be infested; frequently three dozen or more parasites were obtained from the intestine of a single host. These worms were fixed in Heath's and Beauchamp's solutions. Seventy were sectioned serially at 10 μ and stained with Mayer's acid hemalum and triosin. Thirty whole mounts stained with paracarmine were also made. The type material was selected from these prep-

[3] Classification according to Bresslau (1933), with the exception of "Family Anoplodiidae Graff, 1913," which has been rejected in favor of "Family Umagillidae Wahl, 1910b," inasmuch as no reason is given by Graff for discarding the older name or for selecting *Anoplodium* as type genus. The subfamily Umagillinae has been retained as designated by Wahl, 1910b.

parations. At this time another parasite of *Str. franciscanus* was discovered which differed from *Syndisyrinx* in shape, manner of locomotion, and color. A description of this worm is being prepared and preliminary examination of sectioned material indicates a close relationship to *Syndesmis echinorum*. Upon the suggestion of Prof. A. R. Moore, who had occasionally observed parasitic worms in *Str. purpuratus* (Stimpson), forty-seven of these urchins were examined. In twenty-nine of them, worms that are very similar to, and may be identical with *Syndisyrinx franciscanus* were present in small numbers.

General Morphology

The living animals are bright red with a dark brown or yellow median longitudinal line which marks the extent of the intestine. The worms are flattened dorsoventrally and have a leaf-like appearance, being rounded at the anterior end and slightly pointed posterad. Individuals vary in size from 2 to 3 mm. long and 1.6 to 2.5 mm. wide. The body is thickest at approximately one-fourth of the distance from the anterior end and at this level measures about 0.5 mm. in the dorsoventral axis. Laterally and posteriorly the thickness of the body diminishes gradually to about 0.2 mm. at the periphery. A ciliated epithelium covers the entire surface; rhabdites and cuticle are lacking.

The mouth is situated on the ventral surface about one-fourth of the distance from the anterior end and a common genital pore opens ventrally at the posterior extremity of the body. The musculature and parenchyma are typical of other Umagillidae. No excretory system was observed. The strongly muscular pharynx is typically doliiform and possesses pharyngeal glands; it communicates by a short oesophagus with the gut. The intestine, possessing a number of small lateral diverticula, extends posterad under the dorsal epidermis along the mid-line and terminates one-quarter of the distance from the posterior end of the body. The gut contains no permanent lumen and food masses lie in temporary cavities surrounded by large digestive cells. The brain, composed of two cerebral ganglia connected by a wide commissure, lies anterior to the pharynx and gives off paired anterior, lateral, and posterior nerves.

Lobed testes lie lateral to the mid-line in the anterior half of the body. Accessory glands empty into the sperm duct that arises from each testis and passes anterad. These paired tubes unite mesially and enter a small spermiducal vesicle that is continued posterad as a muscular common sperm duct which lies dorsal to the uterus along the mid-line. This tube terminates in an elongated cuticular stylet, the penis, which is enlarged and funnel-like at the base. The penis stylet enclosed in the male antrum extends through the posterior third of the body to the common genital antrum and over most of its length does not exceed 3 μ in diameter.

Paired vitellaria are found immediately posterior to the testes; they are greatly ramified and fill most of the ventrolateral spaces in the middle third of the body. Posterior to the vitellaria a pair of ovaries is located, one on each side of the mid-line. Laterally each branches into five or more finger-like lobes. Three or four collecting ducts from the vitellaria empty with the ovaries and seminal receptacle into the anterior end of the ovovitelline duct. The seminal receptacle is oval and filled with sperm. Located posterodorsad to this organ is a vesicular, sperm-filled bursa seminalis connected to the seminal receptacle by a fine cuticular insemi-

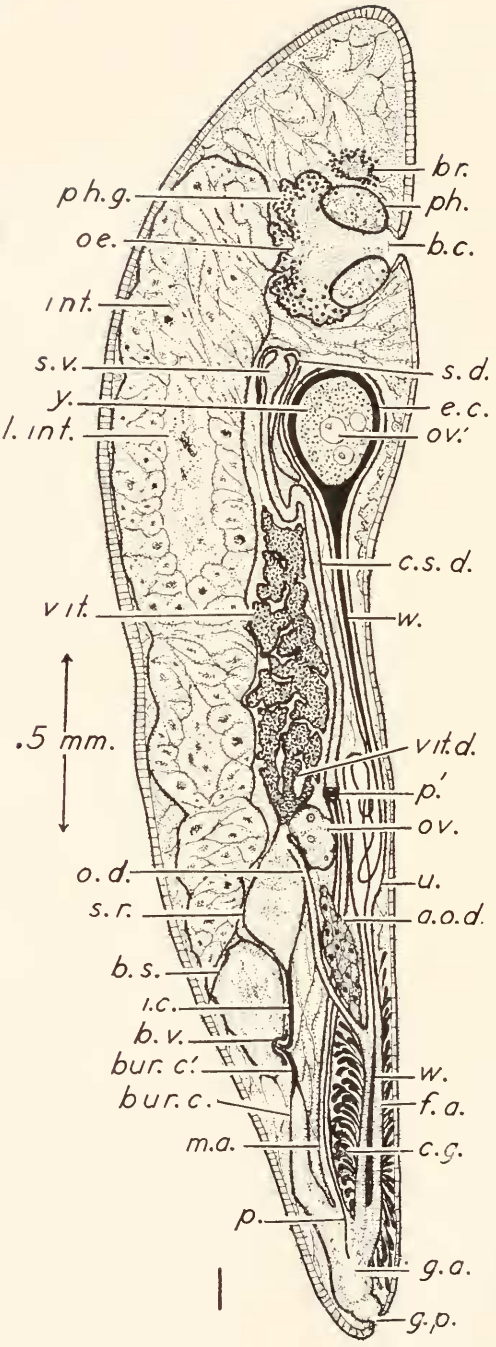

FIGURE 1. Semidiagrammatic median sagittal section.

nation canal. Arising in close association with this tubule is a similar duct, the cuticular proximal part of the bursal canal that passes posterad from the bursa seminalis approximately 60 μ before widening into the posterior muscular portion of the bursal canal (vagina). A cuticular sheath surrounds the openings of these two ducts into the bursa seminalis. The composite structure, consisting of this sheath and the canals passing through it, makes up the bursal valve.

An ovovitelline duct, into which accessory glands empty, arises ventrally at the anterior end of the seminal receptacle. It passes posterad and unites with the female antrum. The uterus, lying close to the ventral epidermis, extends anteriorly from the female antrum almost to the pharynx. At the anterior end of the uterus an egg capsule containing from one to five ova and numerous yolk cells is generally found. The capsule is continued posterad as a long coiled whip similar to those found in related forms. Most of the ventrolateral spaces of the posterior third of the body are filled by cement glands; they communicate by many small ducts with the female antrum. The common genital antrum is an elongated cavity at the posterior end of the body into which the female antrum enters ventrally, the male antrum and penis open mesially and the bursal canal is given off dorsally. At its posterior end is the common genital pore which opens ventrally to the exterior.

Histological Structure

Epidermis

A ciliated epithelium covers both dorsal and ventral surfaces of the body. No pigment or special gland cells were observed in this layer and a cuticle and rhabdites are lacking. The cytoplasm of the cells in the epidermal layer is granular and cell boundaries, though faintly stained, are distinct. The cells covering the dorsal surface are cuboidal and measure 10 μ from basement membrane to external surface. The cytoplasm of these cells stains moderately with hematoxylin. On the ventral surface the cells are flattened and are about 7 μ thick and from 12 to 35 μ wide; they have little affinity for hematoxylin. Cilia of the ventral epidermis are about 6.5 μ long and are almost twice the length of those found on the dorsal surface. Cells possessing the staining properties and short cilia characteristic of the dorsal layer extend for a short distance ventrally around the lateral edges. A zone 4 to 6 cells wide of intermediate nature accomplishes the transition between typical dorsal and ventral epithelium.

Musculature and parenchyma

The arrangement of the musculature is essentially the same as that described for other Umagillidae. Under the basement membrane of the surface epithelium is

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Abbreviations for Figures 1 and 2.

a.o.d.—accessory glands of ovovitelline duct, a.s.d.—accessory glands of sperm duct, br.—brain, b.c.—buccal cavity, bur. c.—bursal canal, bur. c'.—cuticular end of bursal canal, b.s.—bursa seminalis, b.v.—bursal valve, c.g.—cement glands, c.s.d.—common sperm duct, e.c.—egg capsule, f.a.—female antrum, g.a.—common genital antrum, g.p.—genital pore, int.—intestine, i.c.—insemination canal, l. int.—lumen of intestine, m.a.—male antrum, oe.—oesophagus, ov.—ovary, ov'.—ovum, o.d.—ovovitelline duct, p.—penis, p'.—base of penis, ph.—pharynx, ph. g.—pharyngeal glands, s.d.—sperm duct, s.r.—seminal receptacle, s.v.—spermiducal vesicle, te.—testis, u.—uterus, vit.—vitellaria, vit. d.—vitelline ducts, w.—whip of egg capsule, y.—yolk cells.

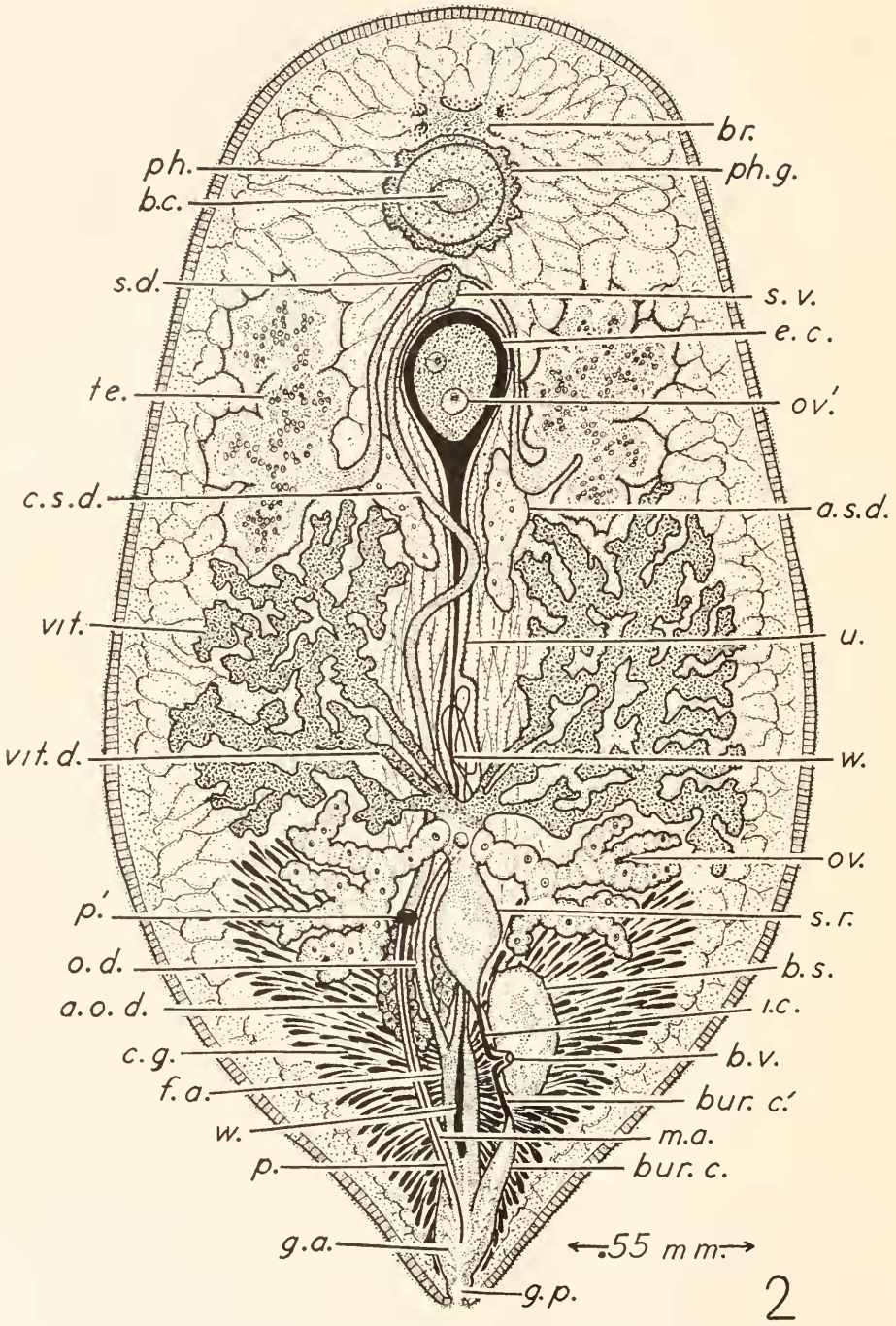

FIGURE 2. Semidiagrammatic median frontal section, intestine omitted.

found a thin layer of subepidermal muscles (Figs. 3–5, 7, 8). The superficial muscles are circular; these overlie a longitudinal sheet, and interposed at intervals between these layers are well-developed oblique fibers. In addition to these, bundles of fibers attached to the internal organs or the basement membrane of the epidermis pass dorsoventrally through the parenchyma (Figs. 1–3). The special muscles of the reproductive and digestive systems will be described in connection with the organs with which they are associated.

A parenchyma, composed of large, irregularly shaped cells with coarsely granular or vacuolated cytoplasm, fills most of the spaces between the internal organs and epidermis. A histologically distinct parenchymatous mass of cells enclosed in a fibrous capsule extends posterad along the mid-ventral line from the posterior level of the pharynx to the region in which the female antrum enters the common genital antrum. The flattened, nonvacuolated cells of this tissue possess finely granular cytoplasm and are arranged in concentric layers around the reproductive ducts, most of which pass through the mid-ventral parenchyma (Figs. 3–5, 7). Nowhere within the parenchyma were flame cells or collecting ducts of an excretory system observed.

Nervous system

The brain is similar in all respects to those described in other members of the family. It is located just anterior to the pharynx and consists of two ganglia connected by a wide commissure. Around the central fibrous mass of the brain are numerous ganglionic cells that stain quite evenly with hematoxylin. Poorly developed anterior, lateral and posterior pairs of nerves leave the brain and can be traced for short distances into the parenchyma. No theca separates the brain or nerves from the parenchyma and no special sensory organs were found.

Digestive system

The mouth lies on the ventral surface about one-fourth of the distance from the anterior end of the body. It opens into a very small buccal cavity lined by flattened ciliated cells that are continuous externally with the ventral epithelium (Figs. 1, 8). A sphincter underlying the epithelium regulates the size of the oral opening. Lying immediately dorsal to the mouth and opening into the buccal cavity is the doliiform pharynx which has the appearance of a dorsally compressed sphere. Its dorsoventral axis is about 0.1 mm. long and its greatest diameter is about 0.17 mm. Passing dorsoventrally through the pharynx is a funnel-shaped lumen that is narrowest at the oral or ventral end. The musculature of the pharynx is similar in most details of its organization to that found in *Syndesmis* as described by Russo (1895). A thin superficial layer of vertical fibers overlies the well-defined muscles encircling the lumen of the pharynx. In addition to the circular and vertical muscles, radial fibers pass from the lumen to the peripheral surface of the pharynx. Nonmuscular cells with heavily staining reticular cytoplasm fill the spaces between the radial fibers (Fig. 8). Surrounding the pharynx is a sharply defined basement membrane to which are attached numerous short, radially arranged, protractor muscles that extend to the basement membrane of the ventral epidermis. The more oblique of these fibers serve also as dilators of the pharynx. Poorly developed retractors are attached to the equator of the pharynx and pass to the dorsal surface. Pharyngeal glands are present encircling the dorsal end of the pharynx. The

peripheral contours of these glands are lobular and a thin basement membrane separates them from the parenchyma. The cells which make up these glands have indistinct cell boundaries and dense cytoplasm containing numerous granules that stain darkly with hematoxylin. Cytoplasmic continuations of the cells extend ventrally and line the lumen of the pharynx (Fig. 8). Leading dorsad from the pharynx is a short oesophagus which passes through the pharyngeal glands and opens into the anterior end of the intestine.

The intestine lies along the mid-line under the dorsal epidermis and extends posterad from the level of the brain to about one-fourth of the distance from the posterior end of the body (Fig. 1). The width of the gut varies from 0.1 to 0.2 mm. at the anterior end and diminishes gradually posteriorly. Short diverticula extend laterally on each side. The epithelium of the intestine is made up of large irregularly shaped cells containing moderately granular cytoplasm. The basal end of most cells reaches the fibromuscular investing sheath of the intestine that separates it from the parenchyma. The lumen of the intestine can only be observed when ingested material is present; this condition is similar to that found in some alloeocoels. In an animal that has been feeding, food masses often lie in cavities that have lost all direct communication with the oesophagus (Fig. 1). Food vacuoles of varying sizes are generally present in the cells surrounding the ingested material and digestive cells were occasionally observed that had apparently migrated into the food masses by amoeboid movement.

Male reproductive system

The paired testes lie lateral to the mid-line in the anterior half of the body. They are approximately 0.5 mm. long and from 0.3 to 0.5 mm. wide. Each is made up of four to six vesicular lobes, the lumina of which are in direct communication with one another (Fig. 2). Separating the testes from the parenchyma is a fibrous sheath that pentrates and partially subdivides the lobes. The chambers so formed are filled with developing germ cells and tangled masses of mature spermatozoa (Fig. 3). Mature sperm are present in all lobes but are more numerous midway between the anterior and posterior ends of the testes near the wide openings of the sperm ducts. These ducts run mesially from the testes and enter the mid-ventral parenchyma, whereupon they diminish to about 10 μ in diameter and generally continue their course anterad, dorsolateral to the uterus (Figs. 1–3). A thin epithelium surrounded by loose fibromuscular elements makes up the walls of the sperm ducts. Near the origin of these ducts from the testes, glandular cells that probably possess some accessory function are found in the mid-ventral parenchyma adjacent to the ventral walls of the tubes (Fig. 2).

At varying distances posterior to the pharynx the sperm ducts unite mesially and enter the anterior end of a common sperm duct which at this point is somewhat enlarged to form a small spermiducal vesicle (Figs. 1–3). The slightly coiled common sperm duct continues posterad from the vesicle through the mid-ventral parenchyma. It gradually diminishes in diameter from 45 μ to 12 μ. Its walls are composed of connective tissue cells surrounded by a sheath of circular, oblique, and longitudinal muscle fibers. The lumen of the tube is lined by a thin squamous epithelium that is separated from the theca by a thick basement membrane. Posteriorly, the common sperm duct unites with the enlarged base of the penis at

about one-third of the distance from the posterior end of the body (Figs. 1, 2, 4). The penis lies in a muscular sheath, the male antrum, which is a diverticulum of the genital antrum. Histologically this sheath is similar in most details of its structure to the common sperm duct; however, the lining epithelium of the male antrum is thicker, in some regions almost occluding the lumen, and a thick basement membrane is lacking (Fig. 5). The copulatory organ is a cuticular tubule that extends through the posterior third of the body and is about 3 μ in thickness over most of its length. The lumen of the stylet does not exceed 2 μ in diameter except at the anterior end of the penis which is enlarged to 12 μ at its union with the posterior end of the common sperm duct (Figs. 1–3). The rim of the funnel-like base of the penis is thickened to form a collar; longitudinal muscles in the walls of the male antrum and common sperm duct attach to this collar and function as protractors and retractors of the penis.

Female reproductive system

The paired ovaries lie in the posterior third of the body. Each is made up of from five to ten lobes that branch dichotomously from common trunks arising near the anterior end of the seminal receptacle. The lobes of the ovaries are directed posterolaterad and are separated from the parenchyma by a very poorly developed theca. The branches are made up of dovetailed chains or rouleaux of compressed ova that are proliferated from primordial cells at the distal ends of the lobes (Fig. 2). Mature ova are approximately 75 μ in diameter and vary in thickness from 20 to 60 μ. The cytoplasm of immature eggs is at first homogeneous, but as development continues many small peripherally distributed granules appear that are probably stored nutrient materials. During the period of growth the nuclei of the ova increase from 7 to 25 μ in diameter and the chromatin granules gradually lose their affinity for basic dyes. In mature ova only the spherical or oval nucleolus stains deeply with hematoxylin (Fig. 4).

A pair of greatly branched vitellaria lie anterior to the ovaries and fill most of the ventrolateral spaces in the middle third of the body (Figs. 1, 2). Many of the dorsoventral muscles of the parenchyma contribute fibers to the diffuse sheath that encloses these ducts. Primordial cells at the distal ends of the branches give rise to yolk cells. As the cells increase in size, the cytoplasm which at first is homogeneous, becomes filled with refractile granules that coalesce to form amber-colored droplets (Figs. 3, 4). From each side three or four collecting ducts packed with mature yolk cells pass posterad from the vitellaria and unite near the mid-line shortly before emptying into the anterior end of the ovovitelline duct (Fig. 2).

The seminal receptacle is somewhat oval and lies ventral to the intestine within the sheath that surrounds the gut. Its anterior extremity is about one-third of the distance from the posterior end of the body. The posterior part of this organ is thin walled and masses of mature spermatozoa are observable in its extensive lumen. Anteriorly the seminal receptacle opens with the paired ducts of the vitellaria and ovaries into the ovovitelline duct which arises ventrally in this region (Figs. 1, 2). The wall of the anterior third of the seminal receptacle is lined by large gland-like cells that restrict the lumen to a narrow channel 6 to 10 μ wide which connects the posterior vesicular portion to the ovovitelline duct (Fig. 4).

The bursa seminalis lies dorsal to the vesicular portion of the seminal receptacle. It is enclosed in the same sheath that surrounds the seminal receptacle and the pos-

terior end of the intestine (Figs. 1, 2). The large lumen of the bursa seminalis is lined by an epithelial layer very similar to that lining the posterior part of the seminal receptacle. In every specimen examined spermatozoa were found in the bursa; frequently they were aggregated into roughly spindle-shaped masses in which degenerating sperm were observable (Figs. 5, 6). Arising ventrally, or in some cases laterally, from the wall of the posterior half of the bursa seminalis is the insemination canal, a fine cuticular tubule about 4 μ in diameter connecting the lumina of the bursa seminalis and seminal receptacle. In close association with the insemination canal, a second cuticular tube of the same dimensions arises from the wall of the bursa seminalis and connects the bursa posteriorly to the bursal canal (Figs. 1, 2, 5, 6). Surrounding the ends of the ducts as they penetrate the lining epithelium of the bursa is a cuticular sheath, 7 μ in diameter and 10 μ long. The inner end of this sheath is involuted and fused to the ends of the two ducts (Fig. 6). To designate this composite cuticular structure made up of the insemination canal, the proximal end of the bursal canal and the sheath surrounding the ends of these ducts, the term, "bursal valve," is suggested.

The bursal canal (vagina) is a tubular structure about 0.1 mm. long and 20 μ in diameter that arises as an anterodorsal continuation of the common genital antrum. Its wall is composed of an inner epithelial layer surrounded by a strong fibromuscular sheath. At the posterior end of the canal the epithelium possesses cilia-like projections characteristic of the lining of the common genital antrum. Anteriorly the lumen of the canal is reduced and the thin basement membrane underlying the epithelium becomes continuous with the cuticular wall of the tubule leading into the bursa seminalis.

A flattened muscular ovovitelline duct (ductus communis) arises ventrally near the anterior end of the seminal receptacle and receives the ducts of the ovaries and vitellaria. It passes posterad through the mid-ventral parenchyma to about the level of the posterior end of the bursa seminalis and here enters the anterior end of the female antrum (Figs. 1, 2, 5). The ovovitelline duct is approximately 35 μ wide but is capable of considerable expansion to allow ova and yolk cells to pass into the uterus. Circular, oblique and longitudinal muscles are observable in contact with the thin basement membrane that underlies the lining epithelium; no fibrous sheath separates this duct from the cells of the mid-ventral parenchyma. Running parallel to the ovovitelline duct in the lateral parenchyma are paired accessory glands which enter the posterior part of the duct prior to its union with the female antrum (Figs. 1, 2, 5). Generally the cytoplasm of these gland cells stains evenly; however, in some cases the cells were observed to be filled with eosinophil granules.

The uterus arises ventrally from the anterior end of the female antrum. It extends anterad almost to the pharynx through the mid-ventral parenchyma and

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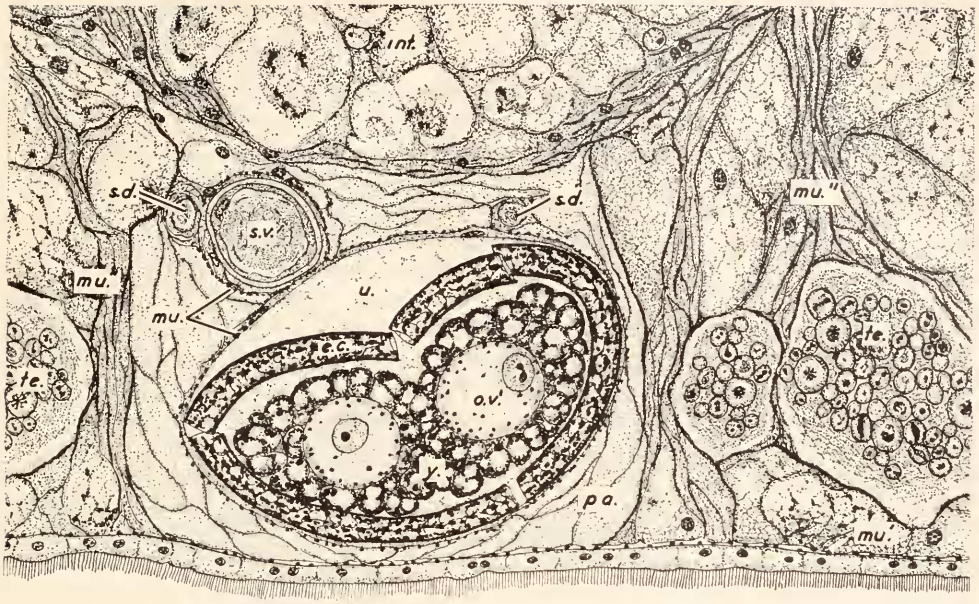
FIGURE 3. Transverse section through egg capsule and spermiducal vesicle (× 350).
FIGURE 4. Transverse section through entrance of ovary into seminal receptacle (× 500).

Abbreviations for Figures 3 and 4.

a.o.d.—accessory glands of ovovitelline duct, c.g.—cement glands, e.c.—egg capsule, int.—intestine, mu.—muscle sheath, mu'.—subepidermal muscles, mu''.—dorsoventral muscles of parenchyma, ov.—ovary, ov'.—ovum, p'.—base of penis, pa.—mid-ventral parenchyma, s.d.—sperm duct, s.r.—seminal receptacle, s.v.—spermiducal vesicle, te.—testis, u.—uterus, w.—whip of egg capsule, y.—yolk cells.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FIGURES 3–4.

through its entire course lies very close to the ventral surface of the body (Figs. 1, 2, 4). The anterior end of the uterus is enlarged and encloses an amber-colored, oval egg capsule containing numerous yolk cells and from one to five spherical eggs (Figs. 1, 2, 3). The egg capsule is cuticular and possesses a whip-like prolongation that extends posterad through the entire length of the uterus and female antrum. Over most of its length the whip is about 10 μ thick. In the middle portion of the uterus the whip is often coiled back upon itself a number of times so that its total length may greatly exceed that of the uterus (Figs. 1, 2). The uterine wall is very similar in structure to the ovovitelline duct and is able to enlarge greatly to accommodate the egg capsule and the folded part of the egg whip (Figs. 3, 4).

The female antrum extends from the posterior ends of the uterus and ovovitelline duct to the common genital antrum (Figs. 1, 2). The walls are lined by columnar epithelial cells surrounded by a thin basement membrane and a muscular layer that is continuous with the fibers enclosing the uterus and ovovitelline duct. The lumen is about 12 μ in diameter and the posterior end of the egg whip, when present, almost completely fills this space (Figs. 5, 7). The ventrolateral spaces of the posterior third of the body contain numerous unicellular cement glands. The cytoplasm of these cells is generally uniformly filled with small granules that have a strong affinity for hematoxylin. Throughout the entire length of the female antrum many ducts from these glands enter the lateral walls (Figs. 1, 2, 5, 7). The secretions of the cement glands are believed to be associated with the attachment of the egg capsules to the substrate when expelled. Living animals compressed under a cover glass were occasionally observed at low magnification to undergo a series of rapid contractions which resulted in the extrusion of the egg capsule and whip. However, nothing is known about the normal deposition and attachment of the capsules, nor are other details of the life cycle understood.

The common genital antrum lies at the posterior end of the body. It is an elongated tube lined by flattened cells that appear to have cilia about 20 μ long which extend into the lumen (Figs. 1, 2, 7). A diffuse fibrous sheath separates this organ from the parenchyma. The common genital antrum receives the terminal ducts of both male and female reproductive systems: the bursal canal arises from it as a dorsal diverticulum; the male antrum enclosing the penis stylet is given off as a mesial evagination; and the female antrum enters it ventrally. The common genital pore opens on the ventral surface at the posterior end of the body. At this point

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FIGURE 5. Transverse section through bursa seminalis and bursal valve (× 350).

FIGURE 6. Bursal valve (× 1,050).

FIGURE 7. Transverse section through the entrance of female antrum and male antrum into the common genital antrum (× 350).

FIGURE 8. Transverse section through pharynx (× 200).

Abbreviations for Figures 5 through 8.

a.o.d.—accessory glands of ovovitelline duct, a.o.d′.—ducts of accessory glands of ovovitelline duct, b.c.—buccal cavity, bur. c.—bursal canal, bur. c′.—cuticular end of bursal canal, b.s.—bursa seminalis, b.v.—bursal valve, cil.—cilia, c.g.—cement glands, d.c.g.—ducts of cement glands, f.a.—female antrum, g.a.—common genital antrum, int.—intestine, i.c.—insemination canal, l. int.—lumen of intestine, m.a.—male antrum, mu.—muscle sheath, mu′.—subepidermal muscles, mu″.—pharyngeal protractor muscles, n.—nerves, oe.—oesophagus, o.d.—ovovitelline duct, pa.—mid-ventral parenchyma, p.—penis, ph.—pharynx, ph. g.—pharyngeal glands, s.—spermatozoa, s′.—degenerating spermatozoa, u.—uterus, w.—whip of egg capsule.

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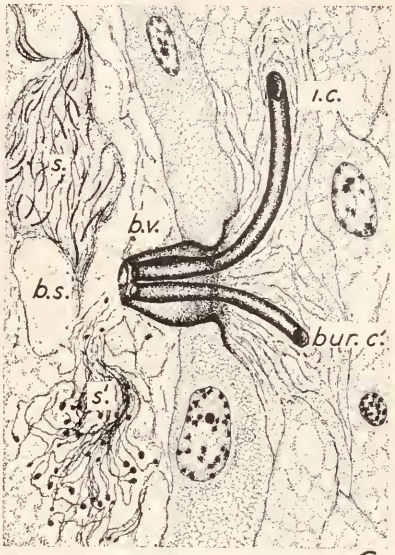

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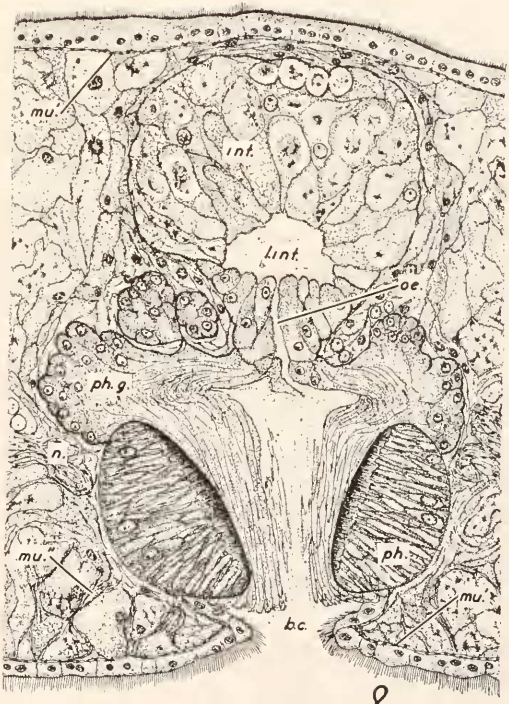

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FIGURES 5–8.

the ciliated ventral epithelium is invaginated and forms a short bulb-like canal which meets an outpocketing of the common genital antrum. Sphincters encircle both ends of this canal and regulate the size of the pore.

Discussion

Comparison of genera

Although the parasite described here is similar in many respects to all genera in the family Umagillidae, there are certain structural characteristics that do not correspond to those of any previously reported genus of this family. Therefore, it is considered necessary to establish a new genus to be designated by the name *Syndisyrinx*. This name is intended to describe the complex bursal valve which is not present in any other genus of the family. The specific name, *Syn. franciscanus,* is given to designate the host, *Strongylocentrotus franciscanus,* in which it was first found.

For the sake of uniformity in the following comparison of genera of the family Umagillidae, the morphological nomenclature used by the various authors in their original descriptions of genera and species has been altered to conform with the terminology employed in the preceding analysis of *Syndisyrinx*.

In addition to the fact that both *Syndisyrinx* and *Syndesmis* are found in the intestine of echinoids, the morphological characteristics of *Syndisyrinx* indicate a closer relationship to *Syndesmis* than to the other genera of the family. The location and appearance of important organs, *viz.*, muscular pharynx, lobed testes, small spermiducal vesicle, muscular common sperm duct, ramified vitellaria, dichotomously branched ovaries, elongated uterus and egg capsule with whip, are very similar in *Syndesmis* and *Syndisyrinx* and strongly suggest a close relationship between these two genera. *Syndisyrinx* differs from *Syndesmis* chiefly in the structure and relationships of the bursa seminalis and seminal receptacle. In *Syndesmis* a single vesicle is present for the reception of sperm and cuticular structures such as the parts which make up the bursal valve of *Syndisyrinx* are lacking. In addition to these differences, the stucture of the penis is markedly dissimilar in these two forms. The penis of *Syndisyrinx* is a cuticular hollow stylet attached only at the base, whereas the copulatory organ of *Syndesmis* is a muscular eversible tube with a cuticular lining (Russo, 1895; Fig. 16).

Structures corresponding to the cuticular canals in the bursal valve of *Syndisyrinx* are found in *Anoplodiera voluta, Wahlia macrostylifera,* and *Desmote vorax*. In *A. voluta* the relationships of the two cuticular canals to the bursa seminalis, as described by Westblad (1930), are very similar to the arrangement of these structures in *Syndisyrinx*. However, the cuticular sheath that surrounds the entrance of these ducts into the bursa is lacking in *A. voluta*. There do not appear to be grounds for concluding that *Syndisyrinx* and *Anoplodiera* are closely related since the appearance and location of the testes and vitellaria, the presence of a single ovary, and the absence of a female antrum connecting the ovovitelline duct and uterus to the common genital antrum in *A. voluta* differ strikingly from the arrangement found in *Syndisyrinx*.

In *W. macrostylifera,* described by Westblad (1930), and *D. vorax,* according to Beklemischev (1916), the proximal end of the bursal canal is cuticular but an insemination canal is lacking. In other respects *W. macrostylifera* differs from

Syndisyrinx chiefly in regard to the morphology of the male reproductive system. The penis stylet is greatly elongated, and paired sperm ducts arising from compact testes unite and communicate by means of a single duct with the large spermiducal vesicle situated anterior to the pharynx. Many points of difference are likewise found by comparing the morphology of *Syndisyrinx* and *Desmote*. The most evident of these are the bipartite gut and the presence of two genital pores, the anterior pore by which the uterus opens to the exterior and the posterior pore which serves for copulation in *D. vorax*.

The other genera of the family lack cuticular parts in the copulatory complex comparable to those in the bursal valve of *Syndisyrinx* and to a greater or less degree exhibit dissimilarities in the location, distribution, number, arrangement and relationships of organs in the body. In these genera the most conspicuous differences with respect to *Syndisyrinx* are: the single ovary and absence of a cuticular copulatory stylet in the genus *Anoplodium;* the unbranched ovaries and double-walled cuticular penis stylet in the genus *Umagilla;* the absence of a cuticular penis and the general arrangement of testes and vitellaria in the genus *Xenometra;* and the single testis in the genus *Collastoma*. A manuscript is in preparation which will deal at greater length with the structural relationships of these forms.

Bursal valve

There is a superficial similarity between the bursal valve of *Syndisyrinx* and the cuticular nozzle-like mouthpieces of acoels. In the acoel, *Amphichoerus,* described by Graff (1891), and many allied forms, one end of the mouthpiece is generally connected to a vesicular sac or bursa filled with sperm; the other end is directed toward the ovary. L. H. Hyman (1937) points out that the function of these mouthpieces is apparently to direct sperm toward the ova to help insure fertilization. This function can hardly be ascribed to the insemination canals of *Anoplodiera* and *Syndisyrinx* which conduct sperm from the bursa seminalis to the seminal receptacle and not directly to the ova; nor does it seem probable that the insemination canals of Umagillidae are homologous to these mouthpieces. Noncuticular ducts connect the bursa seminalis to the seminal receptacle and bursal canal in most genera of Umagillidae, which suggests that cuticular structures are probably of relatively recent rather than primitive origin. In an analysis of the existing genera, Wahl (1910b) presents evidence which leads him to conclude that *Umagilla* is the most primitive and least modified genus of the family. If one accepts this view, it lends support to the opinion expressed above, inasmuch as *Umagilla* lacks any cuticular structures that might be considered homologous to the bursal valve. It is possible that the absence of cuticular parts in some of the species is due to a greater degree of simplification associated with a parasitic existence. However, there is no direct evidence for this supposition, since in the most closely related free-living families, Graffillidae and Dalyelliidae, cuticular structures such as these are not found. This suggests that these tubules have arisen independently, and until additional information is available, the insemination canals and bursal canals of Umagillidae should not be considered as mouthpieces in a true sense.

Although copulation has not been observed in *Syndisyrinx,* it is believed that the sperm of one animal are injected by means of the protrusible penis into the bursal canal of another. Before fertilization can take place, sperm must migrate from the

bursal canal through its narrow proximal end into the bursa seminalis, there remaining until able to find their way through the insemination canal into the seminal receptacle. Evidently many sperm are unable to accomplish this migration and degenerate in the lumen of the bursa seminalis. Sperm that do reach the seminal receptacle must then pass through the constricted anterior part of this organ to fertilize the mature ova that enter the ovovitelline duct at the anterior end of the seminal receptacle.

It is difficult to explain any selective advantage for the presence of the fine canals that make up the bursal valve of *Syndisyrinx*. It was thought at first to be a mechanism for the prevention of polyspermy. However, this explanation is negated by the presence of large masses of spermatozoa in the seminal receptacle. The simplest explanation for the presence of these ducts is that they act as valves which regulate the number of spermatozoa entering the bursa seminalis and seminal receptacle. If this interpretation is correct, it is probable that the function of the bursal valve is to insure a necessary aging of the sperm in the bursa before fertilization. The cuticular walls are necessary to prevent the collapse of these narrow tubes. It is evident that the bursal valve restricts the free passage of sperm from the bursa seminalis and therefore as the result of a single copulation, a continuous supply of sperm may be maintained over a long period of time.

Summary

After completing a histological study of an endoparasitic rhabdocoel from the Pacific Coast sea urchin, *Strongylocentrotus franciscanus,* the following conclusions have been reached:

1. This parasite belongs to the rhabdocoel family Umagillidae but differs in certain characteristics from the eight known genera of the family.
2. The distinguishing characteristics are a single intestine, paired and lobed ovaries and testes, a tubular single-walled cuticular penis stylet, and cuticular ducts connecting the bursa seminalis to the bursal canal and seminal receptacle.
3. A characteristic structure typical of this parasite and not present in other genera of the family is the bursal valve composed of two cuticular tubes, the insemination canal and proximal end of the bursal canal, which enter the bursa seminalis through a cuticular cup-like sheath.
4. The parasite here described is given the name *Syndisyrinx franciscanus, gen. et sp. nov.*

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